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Observations on the Spawning Behavior and Egg Development of *Strongylura notata* (Poey)

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(Plates I & II; Text-figure 1)

Introduction

During extended field work in southern Florida and the Bahamas, from 1928 to 1959 the very common needlefish, *Strongylura notata* (Poey), managed to reproduce close to where our work was being carried out, without yielding easy clues as to the details of this process. Not until 1941 were eggs successfully obtained by stripping[1] and not until 1959 were observations made on reproductive behavior. The places where attempts were made to further these studies include the Florida locations of Key West, the Dry Tortugas, Palmetto Key in Pine Island Sound, Cape Haze on Gasparilla Sound and Manasota Key on Lemon Bay, and the Bahama locations of Nassau, the Berry Islands, Andros Island and Bimini. A preliminary report on the earlier work, Breder (1932), includes data to that date. The present report is released at this time as it is now possible to outline what are evidently the basic features of both egg development and the breeding behavior together with various ecological items and suggestions. It is believed that this may interest and encourage others to notice features of the activities of these fishes that might otherwise be easily missed or ignored. The account of the development of the eggs is based on work done at the Palmetto Key Laboratory of the New York Aquarium. That of the spawning behavior is based on observations made in Lemon Bay from the author's property while working out of the Cape Haze Laboratory.

[1] An amusing account of some of the tribulations incident to the study of these eggs has been given by Bridges (1942).

Spawning Behavior

Although it is not particularly difficult to obtain hatchable eggs from *Strongylura notata* (Poey), by stripping and artificial fertilization, the eggs have not been described, nor has the reproductive behavior. It has long been suspected by the author that these fish spawned in the tangles made by the looping roots of red mangrove, *Rhizophora mangel.* Such a situation practically precludes direct observation. Approach by skiff, close enough to peer into the tangle, scatters the fishes. This is not a matter of sound of oars for it is possible slowly to approach such situations in almost complete silence by drifting in from the proper direction with respect to tidal flow. It is evidently the nearness of the mass of the hull that induces the scattering, principally on an optical basis. A land approach is even worse in this respect as it is impossible to make one's way through the mangroves without considerable commotion. A view from above is precluded by the heavy overhanging foliage. In many places in southern Florida and the Bahamas, it was noted that reproductively-ready fishes would be found in small groups near large mangrove growths always on the lee side and moving in and out of the shelter of the dangling aerial roots.

It was not until a special circumstance arose that the further likelihood of this site of spawning was established and that the actual spawning behavior was observed. In a particular situation on Lemon Bay, Florida, the red mangroves had been stripped off, leaving the black mangrove, *Avicennia nitida,* as the most seaward tree. Here the water surface was fully exposed for observation to the now sandy shore where the water lapped at the pneumatophores. This condition was further enhanced by the incidental presence of a dock running out from shore for nearly a hundred feet. After a rather heavy north wind in mid-April the shore was floored with a deep bedding of samples of the softer algae of the Bay, consisting largely of *Gracilaria.* When the wind veered around to the southwest and became light, on April 19, *Strongylura* began to appear in small bands and hung over the algae beds in the semi-shelter of the overhanging branches of the single black mangrove tree at that point, which is shown in Plate I, fig. 1, as viewed from the dock. By 11:00 A.M. on April 20 a considerable congress had formed at this point. About a dozen of the smaller-sized fishes, believed to be males, hung in a loose aggregation. Occasionally one or sometimes two, larger, fatter fish, believed to be females, would come in from further offshore, swimming usually in a direct line to the aggregation, as though they were certainly directed to it. They would join the group, which would then mill about more actively. See Plate I, fig. 2. One or more of the smaller fish would come up from behind to lie parallel with the larger fish. This action caused an increased milling about, as the fish jockeyed for position. The larger fish would then swim away from the shore, roughly at right angles to it and usually further than the end of the dock, with a varied number of the smaller fish following. These tended to trail behind, sometimes making a troupe of as many as ten, which on occasion fell into single file, although usually the formation was not as regular as that. See Plate II, fig. 3. The remaining aggregation then slowly grew to its former size by the gradual accretion of individual fishes of the smaller sizes which joined the group. It is not clear whether these were the same fish returning or simply new recruits. Later larger fish would join and the whole performance would be repeated. It is practically certain that at least two of the larger-sized fishes returned repeatedly. It is doubted that there was any spawning, but it does seem that this was some kind of pre-spawning maneuvering. It may be that the swimming out to open water by a female served as a cue to the males that she was not quite ready for spawning.

This behavior continued intermittently throughout most of the day. High tide occurred at 1:03 P.M. and low at 7:17 P.M. On the falling tide at 4:00 P.M. spawning or spawning attempts were in progress. Two fish would run side by side between two clumps of red algae and take a momentary stance similar to that taken by *Fundulus,* insofar as their elongate and rather stiff bodies permitted, and "shiver" in appropriate fashion. Before and after such performances, others caused such turmoil by similar but more vigorous activity that the details could not be seen. In all cases of this activity, the fish faced toward shore in three to six inches of water. At no time was there any evidence of wrestling between the males as is done by the related hemiramphid, *Dermogenys,* the nearest relative on which there is any behavior data. The spawning activity continued until darkness at which time all the fish departed. The entire activity occurred in a place that would have been completely hidden from sight if the *Rhizophora* had been left standing.

Wandering bands of *Mugil cephalus* Linnaeus passed nearby these spawning *Strongylura* without heeding them, but after the activity had reached its maximum, the *Mugil* closed in under the spawners and actively fed on something under them, evidently eggs. See Plate II, fig. 4. This went on for some time, not in the least interfering with the *Strongylura* which, naturally, were just under the water's surface most of the time. This area was carefully searched for eggs and later when low tide exposed the place another search was made but without success. Since the eggs are nearly 4 mm. in diameter they should not have been very hard to find if present in any considerable numbers. Since these observations were made at the very onset of the general spring increase in spawning activity, as measured by the nearly total absence of postlarval *Strongylura* from sight observations and from townet material, presumably the egg production was little and probably mostly fell to such fishes as *Mugil.* Two days later the wind swung slowly to the north and in so doing whipped the beach clean of the loose algae. No further activity was seen at that place for the rest of the stay, which lasted for nearly another month. However, observations at a small prominence in Lemon Bay a little north of the site described and of such a nature that it presented *Rhizophora* growth facing in nearly every compass direction, showed that there were similar *Strongylura* gatherings in and about those which happened to be showing a lee exposure and that there were none at places facing into the wind. As noted previously, it was impossible to see just what did transpire in these places. Here again it was impossible to find eggs, although a considerable amount of soft growths, brush and similar things were examined.

Egg Development

The egg development is exceedingly slow, which is in keeping with that of the only other species in the family of which the incubating period is known. Dantan (1905) reported 35 to 36 days to hatching time for Mediterranean *Belone belone* (Linnaeus). Ryder (1882) was only able to carry the eggs of *Strongylura marina* (Walbaum) to nearly seven days, well short of full development. These averaged 3.6 mm. in diameter. Raffaele (1895), Ehrenbaum (1897) and Borcea (1933) all describe the eggs of *Belone,* which are evidently a little less than 2 mm. in diameter. Table 1 and Text-figure 1 indicate the time in days at which various embryological features of *S. notata* appeared. The eggs averaged a little less than 4 mm. in diameter and mean of six 3.95+ and ranged from 3.67— to 4.18—, sank in sea water and possessed rather uniformly distributed adhesive threads which held them in bunches. See Plate II, fig. 5. Eggs taken near Key West, Breder (1932), were smaller, ranging from 3.20 to 3.30 with mean at 3.25 mm. It was impossible to fertilize them because of the absence of ripe males.

The present eggs, the product of a single ripe female seined with a group of males and unripe females on the flats west of Useppa Island in Pine Island Sound late in the afternoon, were fertilized at the Palmetto Key Laboratory at 5:05 P.M. July 5, 1941. The eggs were notably amber-colored. This darkened with the passage of time, which made details of the contents increasingly difficult to discern. It was possible to carry these eggs into the tenth day. Because of practical difficulties it was impossible to keep the temperature as well regulated as desirable in the later portion of the incubation, as may be seen by the temperatures in Table 1. Whether or not this difficulty was responsible for the failure of the eggs to go on to hatching is not known. The experience of Ryder (1882) was rather similar and he presumably supplied his eggs with running sea water or at least had the container in a bath of running sea water.

Most of the details of development are evident from the drawings and Table 1, obviating a lengthy description of the embryological events. It should be noted, however, that only xanthophores were developed, although the embryo had well-developed fin rays and the beginnings of the beak were evident. The reduction of the yolk along with these features of development indicated, however, that the time of hatching was not far distant. Table 2 gives figures of the greatest diameter of the yolk, measured at intervals during the development and an estimation of the volume. As the yolk is normally consumed at an accelerating pace as the embryo grows larger, passing in this instance from a mean of 0.14 mm.^{3} between the first two measurements to one of 1.56 mm.^{3} between the last two, this also suggests the rapid approach of hatching. Also the beak of the smallest certainly identifiable individual of this species, as measured by Breder (1932), had a standard length of 14 mm. and an upper jaw of 1.6 mm. Making measurements in the same way of the drawing in Text-figure 1 F, according to the diameter of the yolk and measuring to the base of the tail, a standard length estimate of 11.6 is obtained with the upper jaw measuring 0.38 mm. Thus in this embryo the beak is 0.03% of the standard length while that of the smallest fish is 0.11%. These various measures taken together suggest that these eggs would hatch, under the specified conditions, in a little more than two weeks.

Discussion

A comparison of the development of the eggs of *Strongylura notata* with that of its more northerly-ranging congener *S. marina* is possible because of the studies of Ryder (1882). The embryologic development is naturally very similar, but the developmental pace is much faster in the former, as is indicated in Table 3. From this it is clear that *S. notata* is developing over twice as fast as *S. marina,* it taking the former only 45.9% of the time it took the latter to reach stage "F."The single negative value in the "Difference" column is accounted for by difficulties in estimating equivalent stages of development and probably does not represent a change in the pace of development. This case, stage "B," the blastodisc, shows little that can serve as a landmark for a comparatively long time. As can be seen from Table 1, the *S. notata* eggs were developing in temperatures not very dissimilar to those in bays where they live, as is indicated by the column of temperatures marked "At dock" compared with those where the eggs were incubating marked "In bowl." Ryder's temperatures, although not given in his paper, were probably at least as close to the Woods Hole water temperatures, very considerably less than those to be expected in the shallow bays of the Florida Gulf Coast. Water temperature records at Woods Hole show that it seldom exceeds 70°, and then only a fraction of a degree, while during the summer the temperatures are mostly in the middle or upper sixties. Compared with this, the temperatures at the laboratory dock side in Pine Island Sound ranged from 73.1 to 80.6. It thus may be that the differences in developmental rates are mostly the result of differences in temperature.

TABLE 1. PROTOCOL OF THE DEVELOPMENT OF EGGS OF *Strongylura notata* (POEY) ARTIFICIALLY FERTILIZED AT THE PALMETTO KEY LABORATORY, JULY, 1941

Hour	Water Temperature		Rate per Minute		Development and Remarks
	At Dock	In Bowl	Heart-beat	Respi-ration	
			July 5		
5.05 p.m.	80.6	79.2			Fertilized.
7:25 p.m.					8 cell stage. Text-fig. 1, A.
7:45 p.m.					16 cell stage.
9:00 p.m.	79.1	75.2			Cells no longer countable.
			July 6		
7:50 a.m.					Germinal disc evident. Text-fig. 1, B.
1:30 p.m.		79.1			G. disc about ¼ down, primitive streak.
5:15 p.m.					Somites and Kupfer's vesicle evident.
8:15 p.m.	73.1	79.1			Blastopore closing. Text-fig. 1, C.
			July 7		
8:00 a.m.		74.2			Eyes forming. Text-fig. 1, D.
10:00 a.m.			102.5		Heartbeat evident.
1:20 p.m.			113.2		Xanthophores appearing.
7:00 p.m.					A few blood cells in circulation.
8:30 p.m.					Slight movements. Plate II.
			July 8		
11:00 a.m.	79.1	74.1	150.0		Xanthophores increasing.
2:30 p.m.		81.2	157.0		Embryo darkening, blood showing many cells. Text-fig. 1, E.
5:00 p.m.		80.1	176.5		Pectorals evident, slight "beak" evident.
8:00 p.m.		78.6	166.7		One egg hatched prematurely.
			July 9		
10:00 a.m.	73.1	77.2	169.4		Pectorals waved, opacity of shell increasing.
6:00 p.m.		80.1	176.5		Tail spatulate, xanthophores more intense yellow.
9:20 p.m.		77.7	153.4		Pectorals waved almost continuously.
			July 10		
7:30 a.m.		75.6	157.0		Pectorals with regular rhythmic movements.
			July 11		
7:20 a.m.		79.2	162.2	34.2	Respiration begun, yolk diameter 2.7 mm.
6:30 p.m.		74.1	142.8	55.0	Eyes darkening.
			July 12		
7:25 a.m.		75.2	133.2	25.4	Iris silvery, fin rays in tail, blood markedly red.

TABLE 1. PROTOCOL OF THE DEVELOPMENT OF EGGS OF *Strongylura notata* (POEY) ARTIFICIALLY FERTILIZED AT THE PALMETTO KEY LABORATORY, JULY, 1941 *(Continued)*

Hour	Water Temperature		Rate per Minute		Development and Remarks
	At Dock	In Bowl	Heart-beat	Respi-ration	
7:45 a.m.		77.1	146.2	75.0	Tail just reaches tip of snout.
			July 13		
7:20 a.m.		77.2	133.2	77.4	Mandibular valves evident and working.
11:15 p.m.		73.1	122.1	53.9	Anal and dorsal rays well developed.
			July 14		
8:45 a.m.		70.1			Diameter of yolk 2.4 mm.
10:30 a.m.			118.0	48.4	
12:20 p.m.		73.5			Beak forming. Text-fig. 1, F. Ribs and neural spines evident.
5:00 p.m.			107.9	25.8	
			July 15		
7:15 a.m.		65.7	100.7		Eyes fully dark.
7:45 p.m.		64.6	85.7	21.8	Yolk diameter 1.9 mm.
			July 16		
7:20 a.m.		64.5	23.1	0.0	Obviously sub-moribund.

It is to be noted that the fish spawning in Lemon Bay were evidently using a site that goes dry at least for intertidal periods and if spawned on a spring tide might be exposed for about two weeks or even more. Also, these eggs have a very long hatching period, something over two weeks under conditions of continual immersion. In view of the fact that they resemble various cyprinodont eggs and there is a variety of morphological reasons to relate the Synentognathi to the Cyprinodontidae, the above conditions suggest that these eggs may be able to stand considerable desiccation in a manner perhaps comparable to those of *Fundulus confluentus* as described by Harrington (1959). It might be that predation on demersal eggs, such as are produced by various species in both these groups, may be less if they are out of or barely in water, rather than submerged to the point of being exposed to the grubbing activity of the large population of *Mugil* and other forms, including a variety of aquatic invertebrates such as the numerous small pagurids, gastropods and small brachyurans. While it is true that the area generally abounds with *Uca*, it is doubtful whether

TABLE 2. REDUCTION OF YOLK WITH DEVELOPMENT IN *Strongylura marina*

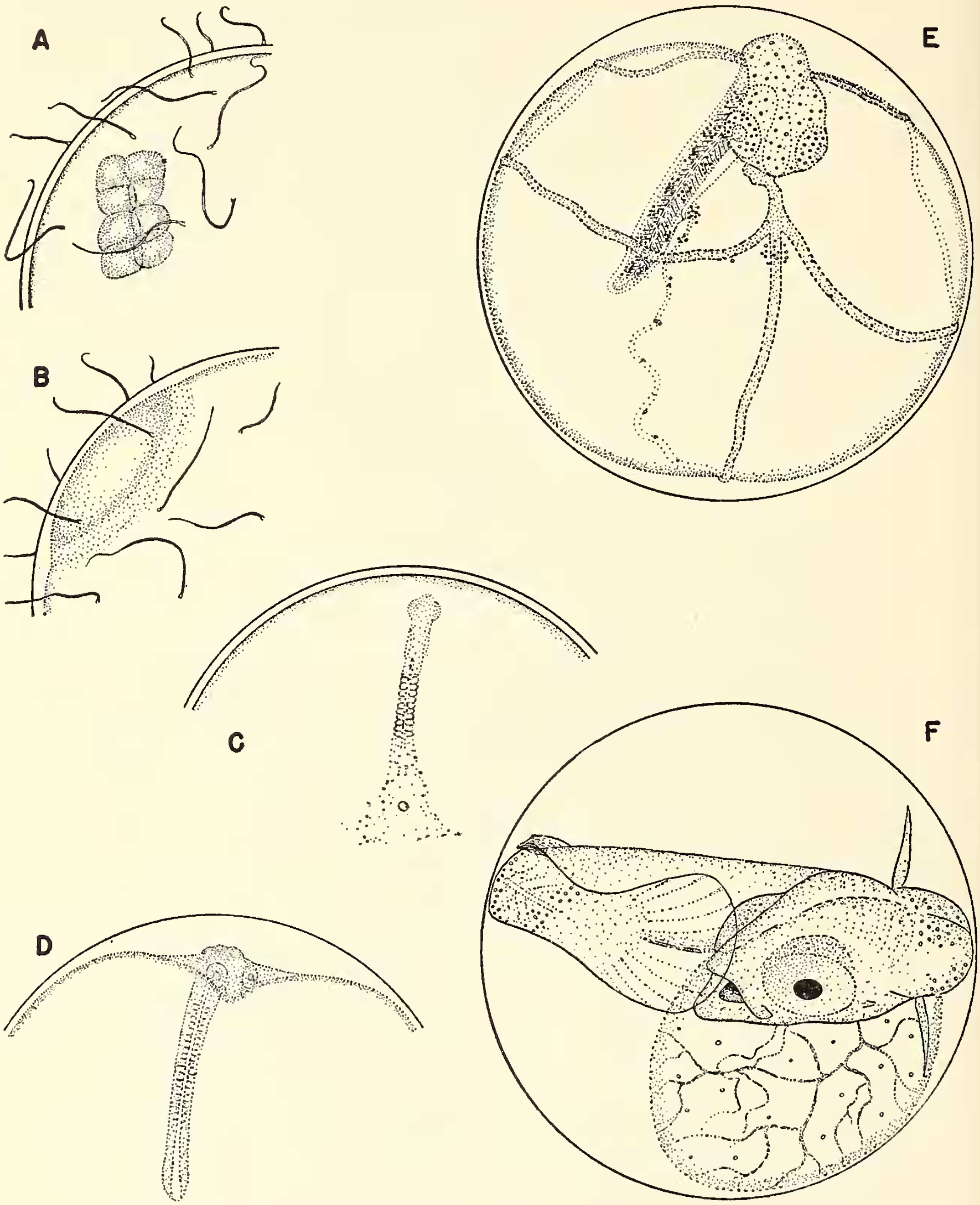
Time is indicated in hours and minutes from fertilization. Volume has been calculated on the assumption that the yolk is spherical, which is as close an approximation as needed for these purposes. Diameter is given in mm. and volume in mm^3.

Time	Yolk Diameter	Yolk Volume
0:00	3.8	28.7
134:40	2.7	10.3
232:05	2.4	7.2
255:05	1.9	3.6

TABLE 3. COMPARISON OF DEVELOPMENT DATA ON *Strongylura notata* WITH THAT OF RYDER'S ON *Strongylura marina*

Time is indicated in hours and minutes from fertilization. Letters in left-hand column refer to illustrations in Text-figure 1. The hours for *S. marina* are to the nearest comparable stages in Ryder (1882).

Stages	*S. notata*	*S. marina*	Difference
"A"	2:20	3:23	1:03
"B"	14:45	10:00	–4:45
"C"	27:10	43:40	16:30
"D"	38:55	70:00	31:05
"E"	71:25	165:30	94:05
"F"	213:15	–	–



TEXT-FIG. 1. Development of eggs of *Strongylura notata*. Times are from fertilization in hours and minutes. The external adhesive threads are shown only in Figs. A and B. The light circles in Figs. E and F represent xanthophores, all in their punctate state. **A.** Eight-cell stage. 2:20. **B.** Blastodisc stage. 14:45. **C.** Segmentation beginning. 27:10. **D.** Eye formation. 38.55. **E.** Advanced embryo with the principal blood vessels indicated. 71:25. **F.** Advanced embryo with much reduced yolk. 213:15.

their numbers or their selectivity for eggs would be as great as that encountered in the totally submerged available sites.

At no time have other species of the smaller inshore species of Belonidae been noted to form aggregations hovering about stands of red mangrove, or any other more or less equivalent shelter, in the manner herein described, although various of them may be swimming by only a short distance away. These include *S. marina, S. ardeola* (Cuvier & Valenciennes) and *S. longleyi* Breder, the spawning sites and habits of which are still unknown.

Summary

1. The eggs of *Strongylura notata* (Poey) go through development typical of their group in a little more than two weeks, at temperatures close to those found in much of their range.

2. Because of the places in which the eggs are spawned, it is suggested that they may be required to withstand considerable desiccation.

3. The spawning behavior is simple and the pairs take a common side-to-side position, forming as much of an "S"-shaped curve as their rather stiff bodies permit.

4. Spawning seems to take place regularly within the tangle formed by the aerial roots of the red mangrove, a situation so sheltered that direct observation is nearly impossible.

5. It appears that spawning always takes place on a lee shore, the least rippling of the surface serving to disperse the spawning groups.

6. No fighting among the males has been noticed, but it would not be surprising if such was found to take place under certain conditions.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. View from dock showing the shore line and the black mangrove tree which provided an inadequate shelter for the spawning of *Strongylura notata*.

Fig. 2. A spawning aggregation over loose algae in the preliminary stages of jockeying for position.

Plate II

Fig. 3. A troupe leaving the shore side aggregation. In this case there are two females, first and last, and five smaller males between them.

Fig. 4. An actively spawning aggregation with a group of *Mugil* feeding beneath.

Fig. 5. Three eggs with active embryos at 51 hours and 25 minutes from fertilization.

Fig. 6. Edge of one egg by transmitted light, showing the distribution of the adhesive threads.